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Consolidation, Reconsolidation of Memory, Extinction and Forgetting: a Review

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Abstract

Introduction. To study the regularities of formation of individual experience we summarize the results of research in consolidation, reconsolidation of memory, extinction and forgetting within a unified idea that considers them in the frames of systems psychophysiology as manifestations of two coordinated processes: formation of new experience and modification of previously formed experience. **Theoretical Justification.** Within the framework of the theory of functional systems, it had been proposed that systemogenesis also takes place in adults, since the formation of a new behavioral act is the formation of a new system. In studies with single-neuron activity recording it was shown that during performance of new behavior the simultaneous activation of multiple earlier formed systems occurs along with activation of new systems formed during learning. Therefore, we consider consolidation, reconsolidation, extinction, and forgetting as manifestations of reorganization of individual experience as a whole. **The results of research** in the neurophysiology of memory show that the processes of memory formation (including its consolidation) and forgetting are not mutually exclusive and can take place independently. Some forms of forgetting are caused by the inability to use memory, rather than by its removal, that makes forgetting similar to the formation of extinction. **Discussion.** We argue that (re)consolidation, extinction and forgetting may be based on similar long-term changes in previously formed experience, in particular those that do not let some elements of this experience to be utilized further.

Keywords

memory, reconsolidation, forgetting, extinction, systemogenesis, learning, individual experience, intersystem relations

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Introduction

A common sense view of a "good" memory is remembering what is needed and recalling it at the right time. Studies of the process of forgetting, including forgetting traumatic events, encourage appreciation of how much memory allows not to recall when it is not necessary. As accurately noted by V. V. Nourkova and A. A. Gofman (2016a), education is aimed mainly at remembering and ensuring its effectiveness, while the "culture of forgetting" is much less pronounced.

Consolidation, reconsolidation of memory, forgetting and extinction are the phenomena that can be labeled as "memory dynamics" (Sozinov & Alexandrov, 2022). Modern researches show that forgetting, including that by interrupting access to some components of memory, is a permanent part of the individual's learning and development, no less significant than memorization.

The goal of this review is to summarize the data from literature on the dynamic memory processes from the viewpoint of learning as a unity of two interrelated processes: formation of new experience and reorganization of the earlier formed experience.

Theoretical justification

The research by our team has led to the development of a system-evolutionary approach (Shvyrkov, 1988; Shvyrkov, 2006; Alexandrov & Krylov, 2005; Alexandrov, 2009; Alexandrov, 2020) and a new discipline – systems psychophysiology. The specific tasks of systems psychophysiology are to study the patterns of formation and implementation of systems, their taxonomy, dynamics of intersystem relations in behavior. These ideas are derived from the theory of functional systems (TFS) by P. K. Anokhin (1968, 1973).

The TFS includes the concept of a factor that forms the system – its result – an adaptive effect achieved during implementation of the system. Consequently, according to the TFS, the determinant of behavior is not the past event (stimulus), but the future event (result). P. K. Anokhin defined a functional system as a complex of selectively involved elements, in which interaction and relation between them is what he called interCOaction (mutual assistance) aimed at obtaining a useful result (Anokhin, 1968). Considering any behavior as goal-directed implies that activity is a fundamental property of living matter; the specific form of activity depends on the level of organization of this matter (Anokhin, 1978). The principle of activity indicates that an individual's action is determined by the future goal (a model of result). The ideas of activity and goal-direction are manifested in the concept of "anticipatory reflection" (Anokhin, 1978). Anticipatory reflection is inextricably linked with subjectivity, since the goals determine the individually specific division of the world, previously (before the appearance of life) "neutral", into "good" and "bad" objects and phenomena that contribute to and hinder the achievement of individual goals. Another basis of this link is that planning of the future (the formation of goals) depends on the the individual memory and motivations (Alexandrov, 2022).

In the activity paradigm, the view on the functioning of an individual, as well as that of a single cell in a multicellular organism, is different from reactivity paradigm. The development of P. K. Anokhin's idea of the "integrative activity of a neuron" (Anokhin, 1975) brought the idea of the determination of neuronal activity in line with the requirements of the systems paradigm by rejecting the consideration of neuronal impulses as a reaction to synaptic input and accepting that a neuron, like any living cell, implements a genetic program and needs metabolites from other cells (Shvyrkov, 2006). In this regard, the sequence of events in the functioning of a neuron becomes similar to the one of an active goal-directed organism, and its impulses are similar to the action of an individual (Alexandrov et al., 1999; Alexandrov, 2008; Alexandrov & Pletnikov, 2022). From this viewpoint, the activity of a neuron is considered as a means of changing the relationship with the environment, directed to the future "action", which leads to the elimination of mismatch between the "needs" of the cell and its microenvironment. The neuron appears not as a "conductor" or "summator", but as an organism within body that provides its "needs" at the expense of metabolites coming from other cells. The neuron satisfies the "needs" of its metabolism by uniting with other elements of the body into a functional system. The consideration of a neuron as an organism in an organism corresponds to evolutionary ideas that imply similarity between the regularities of supporting the vital activity of a neuron and of a single-cell organism. It has been shown that organisms in colonies, including unicellular ones, like cells of a multicellular organism, provide respiration, nutrition and other community functions through cooperation; the metabolisms of individual organisms are synchronized (Grechenko et al., 2013; Weber et al., 2012).

Along with the concept of system, the main ideas that underlie the origins of TFS include that of development, expressed in the concept of systemogenesis. According to this concept, heterochronies in the laying and rates of formation of individual morphological components of the organism at the early stages of individual development are associated with the need for the formation of "whole-organism" integral functional systems that require the involvement of many different elements from a variety of organs and tissues (Anokhin, 1975).

Within the framework of the TFS, the idea that systemogenesis also takes place in adults has been formulated quite long ago (Shvyrkov, 1978; Sudakov, 1979). According to this idea, the formation of a new behavioral act is the formation of a new system. Another fundamental idea is that the differences in the role of individual neurons in execution of behavior should be considered within accounting the history of its formation (Alexandrov, 1989; Alexandrov & Alexandrov, 1982), i.e. the history of successive systemogeneses. The system-evolutionary theory and the system-selection concept of learning have been developed (Shvyrkov, 1986; Shvyrkov, 2006), making it possible to interpret the spiking activity of neurons in terms of the effect of systems and allow us to consider learning as an evolutionary process, part of which is selection. The success of the selection determines the quality of the achieved results and is carried out through individual development, including the formation of "pre-specialized" and "specialized" neurons.

The individual development is a sequence of systemogeneses that underlie the emergence of new relationships with the environment. The formation of a system in the process of systemogenesis is considered as the formation of a new element of individual (subjective) experience in learning. The formation of new functional systems in learning is based on the selection of neurons from the "reserve" (presumably low-active or "silent" cells). The specialization of neurons in relation to a system being formed – system specialization – is permanent. Thus, the new system is an "addition" to the previously formed ones, it is "superimposed" on them.

The neurons are being specialized in relation to the elements of individual experience — the systems formed during individual development, including the individual-specific systems. Therefore, a set of systemic specializations of neurons in each individual is unique. In the studies conducted in our laboratory, the recording of electrical impulses of individual neurons is carried out during the performance of cyclic behavior formed during the learning process. The pattern of systemic specialization of neurons in a given brain area refers to the specific set of the systems in relation to which the neurons of this structure are specialized. The latter is expressed in the fraction of neurons that belong to different systems. The largest number of neurons associated with the functioning of systems of "new" behavior (formed when learning to get food), while in the motor area of the cerebral cortex, neurons of "old" systems predominated (activated, for example, in such acts as any capture of food and non-food objects or during movements) (for example, Alexandrov et al., 1999; Gorkin & Shevchenko, 1996; Kuzina, Gorkin & Alexandrov, 2016; Alexandrov et al., 1993; Alexandrov et al., 2001; Gavrilov et al., 1998; Sozinov & Alexandrov, 2022; Alexandrov et al., 2018).

We have shown that the performance of definitive behavior is underlied not only by the activation of new systems formed during the training of the acts that make up this behavior, but also by the simultaneous activation of many older systems formed at previous stages of individual development (Alexandrov, 1989; Alexandrov et al., 2000; Shvyrkov, 2006). Consequently, the behavioral performance is, so to speak, the performance of the history of its formation–both philo- and ontogenetic, i.e. a set of systems, each being a record of one of the stages of formation of this behavior.

From this statement it follows that the the systemic organization of even outwardly identical actions differs if the history of their formation is different. Indeed, it was shown that the characteristics of the activity of neurons in the cingulate cortex of rabbits specialized for acts of complex instrumental behavior demonstrate significant differences when comparing groups of animals that learn acts of this behavior in a different order (Gorkin & Shevchenko, 1996). In other experiments, a relationship was found between the characteristics of the activity of neurons specialized in relation to the systems of newly formed behavior and the number of stages of learning this behavior (Kuzina & Alexandrov, 2019; Svarnik, Bulava, Fadeeva, & Alexandrov, 2011) Svarnik et al., 2011). In addition, the organization of neuronal activity that underlies outwardly identical instrumental food-acquisition behavior, where training includes different number of stages, turns out to be different (Kuzina & Alexandrov, 2019). Analysis of a set of specialized neurons makes it possible to evaluate "meaningful" changes in behavior — changes in the "state of the subject of behavior" (Alexandrov, 2018), which are described as a set of systems that are simultaneously active in behavior (Shvyrkov, 2006).

Learning begins with a mismatch between the needs of the individual and the possibilities for their satisfaction, which are provided to him by the memory formed at the given moment. This mismatch is manifested at the cellular level in the discrepancy between the metabolic "needs" of the cell and the metabolic influx it receives.

We define learning as system genesis: the process of formation of new functional systems due to the irreversible, lifelong specialization of nerve cells. These cells subsequently provide stability, or "constancy", of memory. Apparently, the activity of specialized cells makes it possible to use elements of experience for the transfer of learning, and also underlies the phenomenology of declarative memory. At the same time, the emergence of new systems entails a restructuring of the individual's experience. Consequently, in the course of individual development, the integral structure of individual experience is constantly changing. One of the manifestations of these changes is forgetting. Experience is changing both due to the "addition" of new systems that appear during learning, and due to the modification of previously formed ones.

The ideas formulated in the framework of the system-evolutionary approach make it possible to generalize the literature and define the similarities and differences between the traditionally distinguished processes of memory dynamics (consolidation, reconsolidation of memory, extinction, forgetting) as different aspects of modifying the structure of experience. We further discuss the studies of each of these processes.

Research results

Memory Consolidation

The fact that memory formation may not be instantaneous was first experimentally shown by G. Muller and A. Pilzeker at the end of the 19th century (Lechner et al., 1999), although the first assumptions on this were formulated much earlier (see Dudai, 2004a). They asked the participants to memorize two lists of meaningless syllables and revealed that if the second list is presented immediately after the first, then the effect of retroactive interference is observed (participants often give answers from the second list when the first one is to be reproduced). However, this effect is not observed if some time passes between memorizing the first and second lists. Thus, it was shown for the first time that memory is formed both during and after learning — in order to transition to a stable state, it must be consolidated (or "become firm" from Lat. Consolidare).

Ideas about memory consolidation have been further developed in studies of the consequences for the recall of new behavior of brain activity impaired by electroconvulsive shock or neurosurgical intervention (for more information, see Grechenko, 1979; Sozinov & Alexandrov, 2022; Corkin, 2002; Dudai, 2012; Eichenbaum, 2013; Squire & Wixted, 2011). These works demonstrated that memory has a stage of formation that takes a certain time and depends on brain processes.

The "standard model" of consolidation attributed a critical role to the hippocampus at the early stages of learning. This role is the activation of neurons in various areas of the neocortex during the reproduction of material. It was assumed that the neuronal changes that allow reproducing the material (the process of "cellular consolidation") occurs faster in the hippocampus than in the cortex, and over time the activation by hippocampus leads to "cellular consolidation" elsewhere — mainly in the neocortex. The process whereby the integrity of hippocampus becomes unnecessary for the recall of this material is called "systems consolidation" (Dudai, 2004b; Runyan et al., 2019). This process, according to the data on distruption and recording of brain activity, can take up to several years in humans (Teng & Squire, 1999) and up to several weeks in rodents (Bontempi et al., 1999). It is believed that this process prevents interference between new and previously formed memories.

A later idea of consolidation, the "multiple trace theory", implies that the hippocampus is always activated during recall (Moscovitch & Nadel, 1998). Consolidation of episodic memory, according to this theory, is based on the formation of many connections between the hippocampus and cortical areas upon the use of this memory (for more information about these and other ideas about consolidation, see: Sozinov & Alexandrov, 2022).

The results of using optogenetic methods correspond to the ideas about changes in the hippocampus and cortex during memory formation (Tonegawa, Morrissey &

Kitamura, 2018). In particular, the suppression of the activity of neurons that were labeled during training impairs behavior, if the suppression has been made at the early stages of consolidation (up to two days) in the hippocampus, and at the late (usually two weeks or more) – in the cortical zones. At the same time, these studies show that the neurons of the cortical regions form the so-called the "silent engram" already at the early stages of consolidation, and in the hippocampus the "silent engram" is revealed at the late stages: such neurons have fewer spikes, but artificial activation of these "engrams" causes recall (Josselyn & Tonegawa, 2020). Consequently, the idea of changing the set of brain structures, on which the recall depends, does not contradict the idea of the irreversibility of the specialization of neurons, introduced here in the "Theoretical foundations". The reorganization of previously formed experience during learning, at least under conditions of our experiments (comparison of the proportion of neurons in the first and second weeks of registration during daily training without changing the task), is not associated with changes in the proportion of neurons specialized in relation to systems of new behaviors (Sozinov et al., 2017).

In contrast to the study of engrams, including those in which neurons are labeled and then artificially activated, and even "false memories" are created (see Josselyn & Tonegawa, 2020), electrophysiological registration of neuronal spikes allows you to determine the specific specialization of neurons in relation to the system of behavioral act and to evaluate sets of specialized cells in individuals with different learning histories. In a study of brain activity during formation of complex behaviors at its successive stages with identifying stable and dyniamic indicators of neural activity, the sets of specialized neurons and neurons with a high probability of activation recorded from the anterior and posterior cingulate cortex zones in rabbits during the performance of food-acquision behavior, we compared between the first and second weeks of the experiment (Sozinov et al., 2015). It was revealed that the "repetition" of outwardly similar behavior does not mean a repetition of the corresponding brain processes. Also, using a similar technique for recording the activity of neurons in the brain of rats, an additional involvement of neurons in the process of specialization that continues during memory consolidation was shown (Kuzina et al., 2015).

Since the effect of consolidation and changes in brain activity associated with the reproduction of behavior at successive stages of consolidation are shown both for declarative memory ("memory systems", see Squire, Wixted, 2011) and for "motor memory" (Brashers-Krug et al., 1996; Shadmehr & Holcomb, 1997; Korman et al., 2003), the consolidation process is considered as a universal pattern of memory formation (see also: Anokhin, 2010; Dudai, 1996). Since the 2000s, the generally accepted ideas about memory consolidation have undergone significant changes. In the case of some authors, these changes affected the general understanding of brain activity, leading to a number of similarities with the concepts developed in systems psychophysiology (Alexandrov, 2005; Alexandrov et al., 2015): the separation of activity related to the actualization of past experience and that related to the formation of a new one (Grosmark, Buzsaki, 2016; McKenzie, Eichenbaum, 2011), linking brain activity not to the reflection of the environment, but to the solution of specific behavioral tasks (Grosmark, Buzsaki, 2016; Weible et al., 2009), dependence of memory reorganization on past experience (Morris, 2006). In addition to the development of ideas about the consolidation process, these shifts were evoked by the studies on memory reconsolidation.

Memory reconsolidation

The phenomenon of temporary vulnerability of memory resumes after a "reminder" - the presentation of one of the components of the learning situation, that is, the recreation of part of the experimental situation. In addition, a reminder presented shortly before retrieval allows the recovery of "forgotten" behaviors that are not recalled without a reminder (Sara, 2000). The resumption of the sensitivity of behavior to interfering influences began to be explained by the "re-consolidation" of memory. It was assumed that when a behavior is reproduced, the memory trace is "reactivated" (used) and again goes into a state whereby changes are possible in it.

Although the reconsolidation effect was first described in the 1960s, the interest in this topic increased mainly in the 2000s (Dudai et al., 2015; Nader, 2015). Specific molecular processes necessary for the consolidation and reconsolidation of memory do not match for all behavioral tasks and brain structures; the speed of these processes and the influence of various learning factors on them are also not the same (see Akirav, Maroun, 2012; Anokhin, 2010; Sozinov & Aleksandrov, 2022).

The effect of reconsolidation is detected not only in animals with the use of pharmacological procedures, but also in humans – in this case, additional learning is used as an amnestic agent. It was shown that the resistance of previously formed behavior to interference vanishes if it is reproduced before learning a new (second) behavior (Hupbach et al., 2008; Lau-Zhu et al., 2019; Walker et al., 2003).

Thus, memory reconsolidation is understood as a process of memory modification similar (but not identical) to consolidation after its reactivation (Debiec et al., 2002; Dudai et al., 2015; Nader, 2003; Walker et al., 2003). Although the effect of reconsolidation is experimentally demonstrated as a violation of recall after a reminder, reconsolidation is considered as a constructive process that allows, if necessary, to reorganize, or "update", previously formed memories.

(Re)consolidation of memory view within systems psychophysiology

From the appearance of the first ideas about the non-instantaneous formation of memory to the present time, memory, as a rule, is considered as preserving a "trace" that the influence of the external environment leaves in the brain structures, or is a model of the external environment. With all the variety of approaches to understanding consolidation (for a review, see: Dudai, 2012), as a rule, long-term strengthening of synaptic conduction in a reflex arc, networks of neurons, etc. is considered as the basis of its regularities.

From a systemic point of view, the neuron is not considered as a conductor of excitation, and the formation of new memory is not considered as creating a neural path or the formation of a "trace" via increasing the efficiency of synaptic communication between the neurons. The formation of memory is the formation of a new system of jointly active cells of the body, including neurons located in different structures of the brain, not necessarily directlu connected. This view is derived from the theoretical positions of the systems approach and from the data obtained within its framework (Alexandrov, 2005; Alexandrov et al., 2018; Alexandrov & Pletnikov, 2022), as well as the results of other studies (for example, Horn, 2004).

The systemic description of consolidation, from our viewpoint, includes two groups of inextricably linked processes: the processes of systemic specialization, i.e. morphological and functional modification of neurons associated with their involvement in a newly formed system; and accommodative reconsolidation. In order to introduce the second group of processes, it is necessary to take into account that the formed memory is not immutable, it is constantly being modified (Alexandrov, 2022; Alexandrov et al., 2015).

Activation of memory, as well as its formation, requires protein synthesis for reconsolidation processes, which, as we pointed out above, are similar to consolidation processes, although not identical to them. Thus, protein-dependent consolidation processes are associated not with a "new", but, more broadly, with an "active" memory (Nader, 2003).

Ideas about accommodative reconsolidation do not contradict the position about the constancy of the systemic specialization of neurons. Reconsolidation does not cancel the modifications that caused the formation of long-term memory (Nader et al., 2000). For a neuron, it is another stage of differentiation, perhaps less extensive than its specialization in learning.

We consider learning as the specialization of a new group of neurons in relation to the system being formed and the "addition" of the latter to previously formed systems. This addition requires mutual coordination of the new element with the previously formed ones and leads to their reconsolidational modification (Alexandrov, 2022; Sozinov, Alexandrov, 2022; Alexandrov et al., 2001). Currently, the results of research on memory reconsolidation lead other authors to the assumption that reconsolidation is indeed a common mechanism for the reorganization of previously formed memory during the formation of a new one (Hupbach et al., 2008).

Earlier, we presented data indicating that neurons belonging to a system and involved in providing one behavior, do not change their system specialization, but rebuild their activity, when this system is included in providing another behavior (Alexandrov, 1989). Later, in experiments with acute (Alexandrov et al., 2001) and chronic (Gorkin, 2021) registration of neural activity, data were obtained that support the assumption of reorganization of the previously formed system of behavioral act after learning the next act.

The reconsolidational modification undergone by the previously formed "old" system after the appearance of a new system connected with it was called by us the "accommodative" reconsolidation (Alexandrov et al., 2001; Alexandrov, 2022). The results of experiments with mapping brain activity by the expression of "early" genes (the *c-fos* gene) during training also support the assumption of reorganization of the previously formed system of behavioral act after learning the next act (Svarnik et al., 2013).

Thus, the second group of processes – the processes of accommodative reconsolidation caused by the inclusion of the system being formed into the existing structure of individual experience – consist in morphological and functional modification of neurons that belong to previously formed systems. This modification does not change the systemic specialization of neurons. The processes of morphological and functional modification of neurons that can unfold during learning without forming a new system were called "reorganizational" reconsolidation (Alexandrov, 2005; see also Safrazyan et al., 2019).

In most cases, there is no distinction between the processes of system specialization and reconsolidation in the studies of memory dynamics. Neurophysiological, morphological, molecular, biological, and other studies of neuronal modifications during learning confound the first and the second group of processes. A differentiated approach to these modifications is a necessary component of a research program aimed at identifying patterns of memory formation.

Since the formation of a new experience is based on previously formed experience, the specifics of the consolidation process depends on the characteristics of the latter. By isolating the components of the structure of individual knowledge and evaluating their composition in a study that employs strategic game of two partners, it was revealed that at several stages of the formation of new knowledge, the components that underlie previously formed acts of the game are activated within the sets of components of the knowledge structure (Alexandrov, Maksimova, 2003). It has been shown that the consolidation and reconsolidation processes are affected by the history of learning (Alberini, 2005; Krakauer et al., 2005; Tse et al., 2007). Therefore, it is also natural that brain ischemia affects further consolidation of memory (Nikishina et al., 2022). Consequently, one of the key aspects of the learning process is the involvement of the individual's "past" experience (see also Arutyunova, Gavrilov, 2014; Gavrilov, 2007; Krylov, Alexandrov, 2007; Krylov, 2015; Kuzina, 2017; Sozinov, Alexandrov, 2022; Shvyrkov, 2006; Alexandrov, 2008; Alexandrov et al., 2018; Brod et al., 2013; Grosmark, Buzsáki, 2016; Kuhl et al., 2012), leading to its modification (Alexandrov, 1989; Alexandrov et al., 2001; Dudai et al., 2015).

Based on the data provided by us in this section and other results (for more information, see Sozinov, Alexandrov, 2022) it has also been suggested in the literature that memory consolidation, once started, almost never ends (Dudai et al., 2015). It is shown that during this process memory is "freed" from information about the learning context, transformed, symbolized, etc. (see Sozinov & Alexandrov, 2022 for more details). It can be assumed that the contribution of long-term memory to the formation of meaning (Ermakov, Denisova, 2019) is also due to reconsolidational changes. This means that consolidation and reconsolidation of memory are accompanied by "getting rid" of part of the memory, i.e. by forgetting.

The coexistence of the processes of "remembering" and "forgetting" during (re) consolidation corresponds to our idea of learning as a unity of two processes — the formation of new experience and modification of previously formed experience. We consider all the processes that are attributed to memory and describe its dynamics (acquisition, storage, reproduction, forgetting; consolidation, reconsolidation, reactivation) from this viewpoint. According to propositions on the dynamics of memory, it is also believed that the comparison of new and previously formed behavioral acts in terms of the individual experience should be made (McKenzie, Eichenbaum, 2011). It follows that normal (not caused by illness) forgetting is a natural and necessary part of the modification of individual experience.

Adaptive forgetting

Forgetting can be defined phenomenologically as the inability to recall what an individual could recall earlier (Roediger, Weinstein & Agarwal, 2010). Although the benefits of such forgetting are less obvious from everyday knowledge than its harm, forgetting of traumatic events and irrelevant or outdated information and the resulting improved possibility of generalization and memorization possess productivity (Luria, 1994; Parker, Cahill & McGaugh, 2006; Roediger et al., 2010). Therefore, forgetting is considered as an adaptive process necessary for normal memorization (Nurkova, Hoffman, 2016a; Sozinov et al., 2013; Nairne, 2010; Ryan, Frankland, 2022).

Considering forgetting as an adaptive process implies that it is consistent with the behavioral task and depends on previously formed experience. Indeed, the rate of forgetting differs between various tasks that require recall: studies of the "functional decay" of memory have shown that the more often it is necessary to replace certain types of information (for example, when we park a car), the faster they are forgotten (Altmann, Gray, 2002).

The connection of forgetting with the behavioral task is a particular consequence of a more general principle — that of goal-directed behavior, introduced by P.K. Anokhin into the conceptual apparatus of physiological research (Anokhin, 1973) and generally accepted in Russian psychology (which is expressed in the concepts of activity, attitude, dominant, and many others). Classical (Blonsky, 2001; Bartlett, 1995) and later works (Lyaudis, 2011; Schacter & Loftus, 2013) show that memory is not for reproduction of the past, but for adaptation and solution of current and future tasks. Therefore, memories are reconstructions, and they are associated with individual traits and life events (see also Anokhin, 1968; Shvyrkov, 2006; Nairne, 2010). Therefore, the identification of "unnecessary" knowledge occurs with respect to the task being solved by the individual.

Forgetting also depends on the "location" of the forgotten in the structure of experience: using the idea of the hierarchical structure of complex memory episodes, it was shown that the nature of forgetting the material is associated with its level of hierarchy in the structure of the episode (Andermane et al., 2021). The authors claim that forgetting has its own specifics at each level and propose the idea of "holistic" and "fragmented" forgetting.

According to the representational theory of forgetting, forgetting is determined by the type of "cognitive representation" formed during memory acquision (Gamoran et al., 2020). The adaptability of forgetting is also evident in the fact that it is often heterogeneous (different aspects of memory are forgotten at different rates), incomplete, dependent on context and time (see the review on this topic: Nørby, 2020). In addition, forgetting can be intentional: ideas about forgetting as a repression, suppression of memories have been formulated, and studies of intentional forgetting have been conducted (Nurkova, Hoffman, 2016b), including that of individual and collective amnesogenic practices (Nurkova, Hoffman, 2022).

Thus, the reorganization of experience, expressed in forgetting, depends on the task and on the individual structure of experience. If forgetting is a necessary part of the modification of experience, then one of its variants can be considered as the formation of a structure of experience that prevents the activation of some of its elements. The creation of such "access difficulties" is revealed in studies of memory consolidation.

Studies of the brain bases of memory consolidation, for the most part, are based on artificial intervention into the processes necessary for the delayed recall of new behavior (see Grechenko, 1979 on the use of electric shock for this purpose, as well as reviews: Alexandrov, 2005; Anokhin, 1997, 2010; Sozinov, Alexandrov, 2022; Barry & Love, 2023; Dudai et al., 2015; de Oliveira Alvares & Do-Monte, 2021; Runyan et al., 2019, etc.). The blockade of protein synthesis or of receptors in nerve cells during training leads to the impairment of recall of a new successfully learned behavior after a break (usually after a few hours). This effect can be interpreted as forgetting and, according to medical terminology, is classified as amnesia (for example, Kozyrev, Nikitin, 2009). In a number of studies of the features of pharmacologically induced amnesia, it has been shown that "forgetting" in this case is a consequence of the inability to utilize memory. So, using passive avoidance training in chicks (in which they stop pecking a bead that had been previously moistened with a bitter substance: Tiunova et al., 2016; Tiunova et al., 2020) and conditioned freezing (Tiunova et al., 2017) in mice with amnesia caused by blockade of NMDA-receptor, protein synthesis and other molecular processes, the possibility of repeated training of animals was assessed. Upon various periods after the disruption of memory consolidation (2 or 24 hours), the possibility of re-learning was impaired, while learning with other new signals (the color of the presented bead in chicks and sound in mice) in the same experimental model was not impaired. Similarly, suppressing the activity of the neurons that have been active during the formation of a new behavior disrupts not only the recall of this behavior, but also the ability to learn it again (Matsuo, 2015). The authors interpret these data with the idea of memory "allocation" (Matsuo, 2015), according to which one behavior can be provided only by a certain set of neurons (despite the presence of a "reserve" of cells for new learning). The inability to form behavior anew, shown in these studies, means that the corresponding memory is preserved, but cannot be retrieved. Interestingly, the conclusion about the preservation of the "memory trace" has already been made earlier solely on the basis of consolidation studies with electric shock and the author's own data on the electrical activity of invertebrate neurons (Grechenko, 1979).

Memory preservation in amnesia has also been demonstrated using optogenetic methods by identifying so-called "silent engrams" (see Tonegawa et al., 2018). This method makes it possible to influence the activity of neurons in which the early *c-fos* gene was expressed during training. This expression is considered as the unfolding of a molecular genetic cascade of events underlying the process of cell specialization in relation to the newly formed system and the accommodative reorganization of previously specialized neurons (Alexandrov et al., 2015; Svarnik et al., 2011; Alexandrov et al., 2001, 2018). Optogenetic activation of neurons in the dentate gyrus of the hippocampus, active during the training and consolidation disruption procedures in mice, has led to the recall of this behavior even 8 days after training, although without this activation, the animals showed forgetting (Ryan et al., 2015).

Thus, one of the reasons for forgetting may be the formation of such a structure of experience with which the actualization of some elements of new experience (systems) is difficult. At the same time, the presence of these elements can influence the further formation of experience. For example, in a study of the neurochemical foundations of behavior at different stages of its formation (Romero-Granados et al., 2010) using early gene mRNA registration, it was shown that activation patterns during primary learning and learning after complete "forgetting" are similar (activation of the hippocampus, somatosensory and perirhinal cortex), but not identical. It is possible that this difference is due to the active creation of inaccessibility, "isolation" of memory, the molecular foundations of which are studied in the framework of "active forgetting".

The activity of forgetting means that the corresponding biochemical processes require energy and are comparable in complexity to the processes necessary for memorization. It is generally believed that forgetting requires disruption of synaptic connections that were formed during the training of a new behavior, and then the prevention of this disruption should prevent forgetting. Indeed, blocking the endocytosis of AMPA glutamate receptors in the hippocampus of rats leads to the prevention of forgetting the location of objects and of preferring the context in which the animal previously received food (Guskjonen, 2016).

In studies on mollusks (Sangha et al., 2005), fruit flies (Berry, Davis, 2014) and rats (Hardt et al., 2013), based on data on specific neurochemical changes in the brain that accompany decrease in the level of reproduction of new behavior, it has been shown that the blockade of these processes leads to the prevention of forgetting (and also often to the disruption of the formation of new behavior). Based on the data obtained, the authors argue that forgetting cannot be considered a "mistake", a malfunction in memory. On the contrary, it is an active, adaptive and normal process necessary for learning and generalization (see also Quiroga et al., 2008). Moreover, intentional forgetting is based on such active processes (Gallo et al., 2022).

A situation in which a previously formed behavior becomes "unnecessary" and previously performed new behavior is inhibited, is also created with the extinction technique. If one of the reasons for forgetting is a temporary limitation of access to memory, then is this type of forgetting similar or identical to the processes underlying extinction?

Extinction

In the frames of conditioned reflex theory, the extinction of the classical conditioned reflex is a decrease in the expression of a conditioned reaction after the termination of reinforcement. Since "spontaneous recovery" of the reaction often occurs after extinction, I.P. Pavlov believed that extinction is due to "internal inhibition", which does not destroy the formed memory (Pavlov, 1952). Therefore, extinction was initially considered as learning (Bouton, Peck, 1992; Myers, Davis, 2002). Currently, it is known that extinction is not so much "destruction" of memory, as it is formation of a new one.

The fact that extinction is an "overlay" and not the destruction of previously formed nenory, has been repeatedly shown in neurophysiological studies (Berman, Dudai, 2001; Davis et al., 2017; Lacagnina et al., 2019). For example, selective inactivation of neurons that were active during the formation of extinction leads to restoration of previously formed behavior (Lacagnina et al., 2019).

The use of contextual freezing shows that the manifestations of fear before the formation of extinction and after it are provided by different brain processes. In one of these studies, it was shown that the formation of behavior is accompanied by increased fos activation of pyramidal neurons of the basolateral amygdala, and the formation of extinction is accompanied by a decrease in their activation and activation of neurons of the medial prefrontal cortex, the integrity of which is associated with the formation of a new memory for extinction (Davis et al., 2017).

In another study with the same technique, the characteristics of the spines of neurons in two zones of the limbic cortex of mice were evaluated (Vetere et al., 2011). The authors found that only large spines remain in the anterior cingular cortex after extinction, and many new spines appear in the infralimbic zone (compared to the group without extinction). They suggest that spines remain in the anterior cingular cortex after extinction, on which the restoration of behavior depends in the future.

Thus, extinction, like other phenomena of memory dynamics discussed here (consolidation, reconsolidation, forgetting) is one of the variants of changing the structure of individual experience. Extinction is produced by learning — the formation of new systems (due to the specialization of neurons) and modification of previously formed experience (accommodative reconsolidation). Interestingly, consolidation effect has been demonstrated for extinction (see Dunsmoor et al., 2015). Moreover, pharmacological disruption of memory for extinction, simulating active forgetting in drosophila, causes spontaneous recovery of appetitive behavior, and the blockade of active forgetting prevents spontaneous recovery (Yang et al., 2023). Consequently, the formed structure of experience assumes the possibility of restoring behavior and allows freezing and extinction memories to coexist.

Discussion

Similarities and differences of (re)consolidation, extinction, and forgetting

Describing the common features of the processes of memory reconsolidation, extinction and forgetting, L. de Oliveira Alvares and F. Do-Monte (de Oliveira Alvares & Do-Monte, 2021) indicate that after memory consolidation, its subsequent state is determined by its use: if this memory is not “retrieved”, then it is "filtered out" as a result of the processes of active forgetting and interference; after retrieval in a new behavioral situation, the memory is destabilized, and can either be modified if the novelty is insignificant (reconsolidation), or supplemented with a new memory that will prevent the retrieval of the first (extinction). It is noted that the exact knowledge for a clear separation of the two latter processes has not yet been obtained. In particular, the authors point out that the only difference in methods between reconsolidation and extinction is the duration of the procedure of "reactivation" of memory: if the reactivation is short, then memory reconsolidation occurs; if it is prolonged, then extinction occurs (de Oliveira Alvares & Do-Monte, 2021). Next, we will consider a number of studies that point to additional similarities between forgetting, extinction and reconsolidation of memory.

In a series of studies using snails that learn to reject two types of food during pharmacological disruption of reconsolidation, it was shown that amnesia caused by the blockade of protein synthesis before the "reminder" procedure (presentation of one of the foods) is characterized by long-term dynamics: the activity of defensive-behavior neurons during presentation of a juice used as the reminder had been decreasing for seven days (the corresponding indices were recorded 1, 3, 7 and 15 days after the reminder procedure) (Kozyrev, Nikitin, 2009). In other words, the severity of amnesia increased over time. Consequently, the process underlying this amnesia is gradual and depends on protein synthesis. In this sense, the dynamics of the active process of "forgetting" is similar to the dynamics of learning: the inability to reproduce behavior is formed gradually.

In the later stages, amnesia after disruption of the process of reconsolidation is accompanied by the inability to re-learn behavior, that is, in a certain time interval, this amnesia is not only retrograde (the reproduction of previously formed behavior is disrupted), but also anterograde (long-term memory is not formed anew for this behavior) (Kozyrev et al., 2014). These results show that amnesia after a disruption of reconsolidation is a consequence of the lack of "access" rather than "destruction" of memory. Arguments in favor of the assumption that the reconsolidation effect is due not to the loss of memory material, but to the inability to retrieve it have been published before (Amelchenko et al., 2012, 2013; Anokhin et al., 2002; Dudai, Eisenberg, 2004). This statement also follows from the ideas about the constancy of the systemic specialization of neurons, which is being developed in our research (see above in the section "Theoretical foundations"). Interestingly, the severity of anterograde amnesia also depends on the time of amnesia induction after training: it is strongly pronounced and stable if the induction of amnesia was 2 days after training; if it was carried out 10 days after, then amnesia is not detected; however, the induction of amnesia 30 days after training is successful, but is not accompanied by anterograde amnesia (Kozyrev et al., 2014).

Further studies of the molecular bases of the dynamics of amnesia led the authors to the conclusion that the processes of reconsolidation and amnesia are independent, but both depend on protein synthesis (Nikitin et al., 2020). These and other results allowed them to propose that the development of this type of amnesia is similar to the learning process (Nikitin et al., 2020). Thus, this amnesia is specific to the type of food in relation to which it was formed; it depends on protein synthesis (Nikitin et al., 2019) and RNA methylation at a certain time interval (the blockade of these processes leads to a decrease in amnesia and the ability to form behavior if carried out within 9 hours after the disruption of reconsolidation); its severity changes over time (see above in this section); the reminder presented long time after this interval opens up the possibility of disrupting amnesia again with the blockade of DNA methylation (a time-window is opened to reduce amnesia similar to memory impairment after the blockade of protein synthesis during its reconsolidation). Moreover, using this technique, the authors demonstrated an impairment of re-learning not only after disruption of reconsolidation, but also consolidation (Nikitin et al., 2020). At the same time, the impairment of re-learning after reconsolidation of memory is also shown in vertebrates (Tiunova et al., 2022) using the experimental model we discussed above in relation to memory consolidation in chicks (Tiunova et al., 2020).

The processes underlying artificial amnesia may be similar to the processes that cause memory disorders (Nikitin et al., 2020). It can also be assumed that "healthy" forgetting develops in a similar way (Tiunova et al., 2020). In this case, forgetting and extinction are similar not only as alternative ways of changing consolidated memory depending on use (as suggested in de Oliveira Alvares & Do-Monte, 2021), but also as options for such modification of experience that prevents the use of previously formed experience.

It is also important that there are differences between forgetting and extinction. In particular, in case of amnesia, there is no spontaneous recovery of behavior, and in case of extinction, there is the possibility of re-learning (Nikitin et al., 2020). The differences between the processes underlying the phenomena of reconsolidation and extinction have also been shown earlier (Suzuki et al., 2004).

Thus, the process of forgetting, caused artificially by the blockade of molecular processes in the brain, develops as a separate process, the dynamics of which is similar to the dynamics of learning.

The research results discussed here show that forgetting, extinction and learning are variants of experience modification, differing in whether a new element of experience is formed (which is the case during learning and extinction, but not during forgetting), and how previously formed experience is modified, in particular, whether intersystem relationships change (see Yu.I. Alexandrov et al., 1999; I.O. Alexandrov, 2006; Bezdenezhnykh, 2004) so that it hinders the activation of previously formed experience (which takes place with extinction and forgetting, but not with learning). Such rearrangements of intersystem relations may underlie the ability of control of behavior, including that during consealing information (Uchaev, Alexandrov, 2022).

Conclusion

The description of the phenomena of consolidation, reconsolidation of memory, extinction and forgetting using the concepts of systems psychophysiology suggests that all these phenomena are a manifestation of learning, i.e. changing the structure of individual experience due to two processes: the formation of a new experience and modification of previously formed experience that provised coordination with the new one in the case of its formation. During this process, the formation of new experience, on the one hand, is impossible without updating previously formed experience, and on the other hand, leads to its modification, including the one that prevents further updating of a part of previously formed systems.

Reconsolidation of memory implies the presence of a time-window when it is possible to form "restrictions" on the implementation of some elements (systems) of previously formed experience. Apparently, the consolidation of the memory for extinction and the process of forgetting are also based on the possibility of forming such a restriction. Therefore, it can be assumed that reconsolidation, extinction and forgetting are based on similar long-term changes in previously formed experience, which exclude activation of some of its elements.

In systems psychophysiology, learning is considered as an evolutionary process. The increase in the relative number of specialized neurons diring consolidation shown in our laboratory (Kuzina et al., 2004) reveals the course of selection and changes that occur in the neural subserving of new behavior. The data presented in this review show that forgetting and extinction can be a manifestation of the selection process at the system level — the same as selection during learning, when some elements of experience start to be involved in new behavior, but on the opposite: when other elements are gradually eliminated.

Based on this, we can draw the following main conclusions:

- Consolidation and reconsolidation of memory are accompanied by forgetting, i.e. hindering some of the memory components;

- Studies in which forgetting is pharmacologically prevented or enahced show that forgetting can occur by interrupting the "access" to memory;
- Extinction has common features with forgetting, since it is formed as an addition of a new memory that co-exists with a preserved but inaccessible memory for the behavior being extinguished;
- The use of the conceptual apparatus of systemic psychophysiology allows us to describe the phenomena of consolidation, reconsolidation of memory, extinction and forgetting as manifestations of changes in the structure of individual experience via two differently pronounced processes: the formation of new experience and modification of previously formed experience.

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Conflict of Interest Information

The authors have no conflicts of interest to declare.